

MORPHOMETRIC ANALYSIS OF AN AMELANCHIER (ROSACEAE:
MALOIDEAE) COMPLEX ON THE DELMARVA PENINSULA
(DELAWARE, MARYLAND AND EASTERN VIRGINIA)
RESOLVES THE TAXONOMIC IDENTITIES OF
AMELANCHIER OBOVALIS AND A. CANADENSIS

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ABSTRACT

Amelanchier obovalis and *A. canadensis* (Rosaceae: Maloideae) are similar taxa with overlapping geographical ranges on the Atlantic Coastal Plain of the United States. Conflicting circumscriptions, polyploidy, hybridization, and agamospermy may have contributed to the taxonomic confusion in these species. In this study I perform a morphometric examination of these two species on the Coastal Plain of Delaware, Maryland and the eastern shore of Virginia—collectively called the Delmarva Peninsula. I developed a dataset of eleven flowering, fruiting and vegetative characters taken from marked individuals. A second dataset contains six minimally correlated characters that were obtainable from the type specimen of *Amelanchier obovalis*. I use Principal Components Analysis (PCA) to summarize phenetic similarities and dissimilarities between individuals and agglomerative, hierarchical Cluster Analysis to aid in visualization of morphological groups. Selection of groups (putative taxa) to inform a testable group model was performed iteratively using concordance in phenetic methods (PCA and Clustering) and inferential descriptive statistics. Analysis supported a four-group model for which I found a significant overall multivariate effect (Pillai's Trace, $F = 7.29$, $P > F < 0.0001$) using Multivariate Analysis of Variance (MANOVA). Two well-supported groups (1 & 4) corresponded to *Amelanchier obovalis* and *Amelanchier canadensis*. The remainders of the sample are intermediate between *Amelanchier obovalis* and *Amelanchier canadensis* and may be the product of recurrent hybridization between these taxa. Lack of clearly delimited morphological character space and apparent ecological and genetic exchangeability in these taxa suggests the taxonomic rank of variety under the earliest combination in *Amelanchier*, e.g., *Amelanchier canadensis* var. *canadensis* and *Amelanchier canadensis* var. *obovalis* as originally proposed by Michaux (1803). I present a taxonomic treatment and historical analysis of the species taxonomy and a dichotomous key to the varieties.

RESUMEN

Amelanchier obovalis y *A. canadensis* (Rosaceae: Maloideae) son taxa similares con áreas geográficas solapadas en la llanura costera atlántica de los Estados Unidos. Las circunscripciones conflictivas, poliploidía, hibridación, y agamospermia pueden haber contribuido a la confusión taxonómica en estas especies. En este estudio realizo un examen morfométrico de estas dos especies en la llanura costera de Delaware, Maryland y costa este de Virginia—llamados colectivamente Península de Delmarva. He desarrollado un conjunto de datos de once caracteres de flores, frutos y vegetativos tomados de individuos marcados. Un segundo conjunto de datos contiene seis caracteres mínimamente correlacionados que se obtuvieron del espécimen tipo de *Amelanchier obovalis*. Utilizo el Análisis Componentes Principales (PCA) para resumir las similitudes fenéticas y disimilitudes entre individuos y un Análisis de Clusters jerarquizado para ayudar en la visualización de grupos morfológicos. La selección de grupos (taxa putativos) para informar de un modelo de grupo comprobable se realizó iterativamente usando la concordancia en los métodos fenéticos (PCA y Clustering) y estadística descriptiva inferencial. El análisis da un modelo de cuatro grupos para el que encontré un efecto multivariante general significativo (Pillai's Trace, $F = 7.29$, $P > F < 0.0001$) usando Análisis de Varianza Multivariante (MANOVA). Dos grupos muy claros (1 & 4) correspondieron a *Amelanchier obovalis* y *Amelanchier canadensis*. Los restos de la muestra son intermedios

entre *Amelanchier obovalis* y *Amelanchier canadensis* y pueden ser el producto de hibridación recurrente entre estos taxa. La falta un espacio de caracteres morfológicos claramente delimitados y aparente intercambio ecológico y genético en estos taxa sugiere el rango de variedad bajo la combinación más antigua en *Amelanchier*, e.g., *Amelanchier canadensis* var. *canadensis* y *Amelanchier canadensis* var. *obovalis* como fue propuesto originalmente por Michaux (1803). Presento un tratamiento taxonómico y análisis histórico de la taxonomía de las especies y una clave dicótoma para las variedades.

INTRODUCTION

Amelanchier Medic. (Rosaceae: Maloideae) is comprised of deciduous small trees and shrubs of the North Temperate Zone (Phipps et al. 1990). *Amelanchier* flowers are pentamerous, radially symmetrical and protogynous (Robinson 1982; Campbell et al. 1991) arranged as inflorescences of simple racemes (except in *A. bartramiana*). *Amelanchier* fruits are globose, berry-like pomes that attract a wide variety of frugivorous dispersers (Robinson 1986). The leaves of *Amelanchier*, and of the subfamily Maloideae in general, vary greatly in size, shape and dentation, and mature foliage on short shoots is often very different from those on juvenile (e.g., new sucker growth) or long shoots (Robertson et al. 1992). The total enumeration of taxa varies among authors. For example, in the northeastern United States, Landry (1975) recognized six species; Fernald (1950a) includes 19 species but Gleason and Cronquist (1991) only nine species. Synonymy within *Amelanchier* is formidable, reflecting uncertainty surrounding taxonomic concepts of species and infraspecific taxa (see Fernald 1941; 1946). Reproductive biology of *Amelanchier* is characterized by polyploidy, agamospermy and extensive hybridization between most eastern North American species (Wiegand 1912; 1935; Jones 1946; Cruise 1964; Campbell et al. 1987; Weber and Campbell 1989; Campbell et al. 1991; Dickinson and Campbell 1991; Campbell and Wright 1996; Campbell et al. 1997b; Campbell 1999). Recent research has revealed several complex taxonomic issues arising from mating system versatility in the genus including the presence of persistent, morphologically distinctive hybrids, e.g. *Amelanchier* x *neglecta* (Weber and Campbell 1989; Campbell and Wright 1996), microspecies derived from intraspecific hybridization followed by agamospermy, e.g., *Amelanchier* "rubra" (Dibble et al. 1998) as well as wide morphological variation among populations of single species (Cruise 1964; Campbell et al. 1997a). Reproductive versatility in *Amelanchier*, i.e., the combination of vegetative spread, interspecific hybridization and formation of agamic complexes has contributed to their phenotypic diversity and ecological success, particularly in early successional environments (Wiegand 1912, 1935; Cruise 1964; Robertson 1974; Campbell et al 1991; Campbell 1999).

Despite the abundance and ecological importance of *Amelanchier* in the southeastern United States this genus remains poorly studied. This may be due, in part, to the limited field work that the primary authors of the genus (e.g., K.M. Wiegand, G.N. Jones, M.L. Fernald) performed in the southern states but probably more persistently by the difficulty in gathering adequate material for study, and the limited usefulness of herbarium material, including some type specimens, (Wiegand 1912; Nielsen 1939; Fernald 1946; Jones 1946; Cruise 1964).

In a long-term study (1999-present), mainly of the stoloniferous members of *Amelanchier*, the most problematic species for confident identification in the field and herbarium have been *Amelanchier canadensis* (L.) Medic. and *Amelanchier obovalis* (Michx.) Ashe. *Amelanchier canadensis* and *A. obovalis* occur along the east coast of North America with overlapping ranges in the southeastern United States. Herbarium sheets labeled as these species often have multiple annotations and the opinion expressed often seems cor-

related with the general habitat types written on the label and notes on plant habit or height noted by the collector and not their morphological characteristics (C. Frye, pers. obs.).

Three species in addition to *Amelanchier obovalis* and *A. canadensis* are listed in floras (Tatnall 1946, Brown and Brown 1980) specifically covering the geographic region known as the Delmarva Peninsula (Fig. 1), which is comprised of eastern Maryland, Delaware and eastern Virginia (hereafter referred to as the study area).

Amelanchier arborea (Michx. f.) Fernald is a species of dry, upland forests that is excluded in this analysis. *Amelanchier intermedia* Spach, is restricted to the Piedmont and Mountain physiographic provinces (Wiegand 1920) and was not considered here. *Amelanchier stolonifera* Wieg. is cited by Tatnall (1946) from the Piedmont physiographic province in Delaware (not included in the study area). *Amelanchier canadensis* (L.) Medic. var. *subintegra* Fernald (Fernald 1950b) has been observed by the author in the study area but no specimen corresponding to this taxon occurred in the sample.

Shrubs and small trees that key to *Amelanchier canadensis* and *A. obovalis* are widespread and common in the study area but many characters purported to separate the species in taxonomic keys appeared highly variable, temporal, or were the subject of disagreements among authors. Characters such as plant habit (stoloniferous and colony forming versus clumped and multi-stemmed), plant height, and ovary pubescence that are often used in major couplets to distinguish these species I found were difficult to objectively determine. For example, nearly all individuals in the study vigorously sucker but under certain conditions such as mowing and burning form low, shrubby colonies with apparent vegetative spread. Long observation (1999-present) of *Amelanchier* in the study area suggested the presence of at least two coherent taxa; however, several morphologies could not be identified with existing taxonomic keys (Wiegand 1912; Fernald 1950a; Radford et al. 1968; Gleason & Cronquist 1991). Taxonomic complexity in the study area may reflect the presence of numerous distinctive microspecies produced by hybridization events followed by asexual seed production and/or cryptic hybridization involving a number of agamosperms that would be difficult to detect using morphological characters present at a single phenological stage.

This study aims to determine whether *Amelanchier* occurring on the Delmarva Peninsula exists as a complex of intergrading, minimally separable phenotypes or contains two or more well-defined taxa that are significantly different from each other in morphology, ecology or both. In order to examine morphological complexity and evaluate the various treatments of *Amelanchier canadensis* and *A. obovalis* I developed two datasets of morphometric characters. The first dataset comprised a "full" set of flowering, fruiting and vegetative characters taken from marked individuals (Full dataset). The Full dataset was used to explore multivariate relationships between individuals, reduce dimensionality and select taxonomically informative characters. The second dataset comprises a reduced set of characters that includes only those characters present on the type specimen of *Amelanchier obovalis* (Type dataset). The Type dataset is analyzed to determine the taxonomic identity of *Amelanchier obovalis*. A similar analysis using the type of *Amelanchier canadensis* was not possible given the few taxonomically informative characters present.

Due to the complex classification history of *Amelanchier canadensis* and *A. obovalis* I defined groups for analysis *a posteriori*, without taxonomic classification so as to avoid confounding *a priori* taxonomic identity with the partitioning of morphological variation. I use a combination of Cluster Analysis and Principal Components Analysis (PCA)

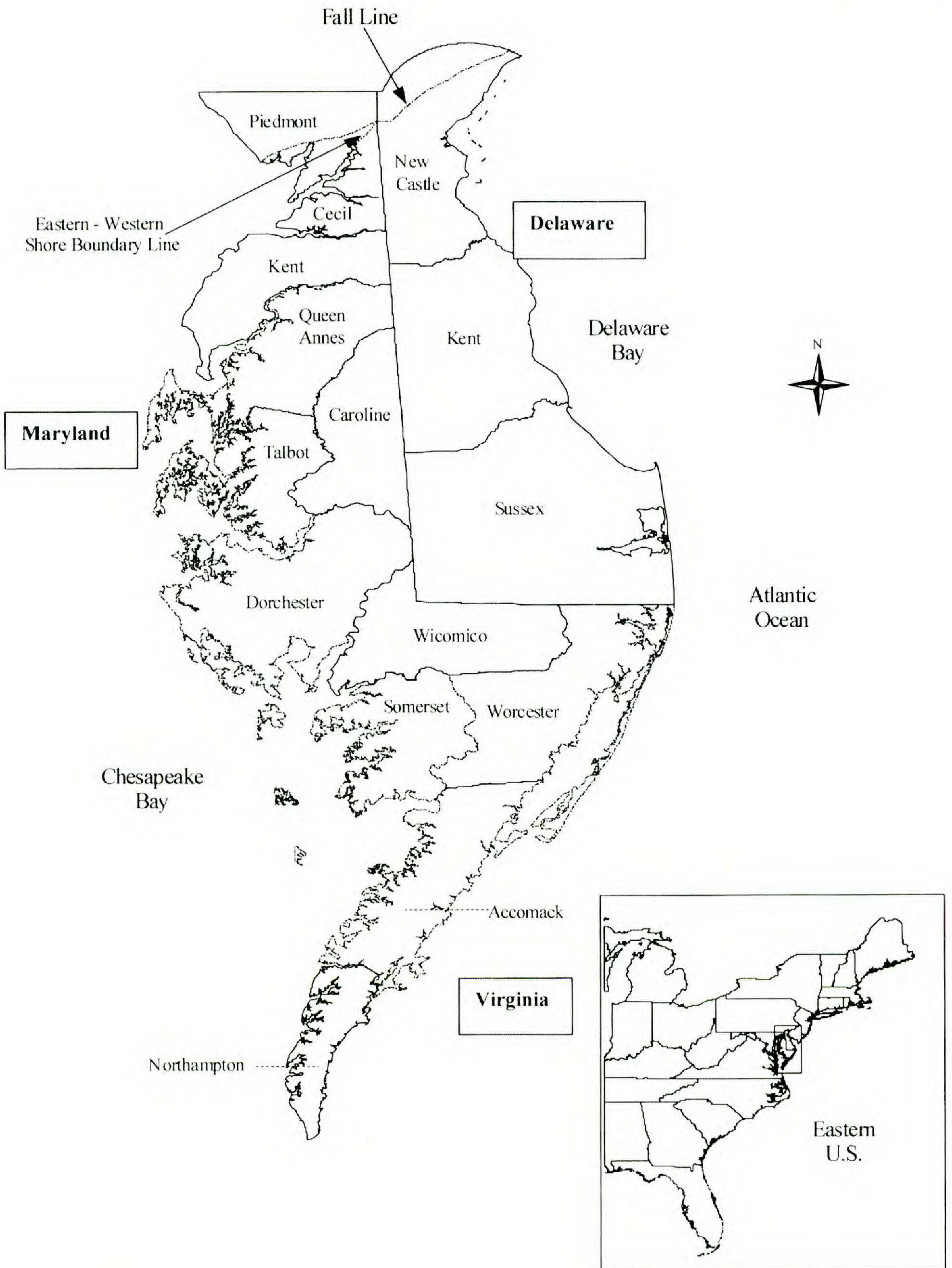


FIG. 1. Geographical location of the study area. The Delmarva Peninsula of the eastern United States comprising Delaware (New Castle, Kent and Sussex Counties), eastern Maryland and eastern Virginia (Accomack and Northampton Counties).

to delimit groups (putative taxa) and Multivariate Analysis of Variance (MANOVA) to test the best-supported group model. Multivariate analysis of morphological data has been used to resolve species complexes in *Amelanchier* (Dibble et al. 1998), classify taxa within groups defined *a priori* (Saarela et al. 2003; Leonard et al. 2005) and to resolve difficulties caused by morphological overlap in infraspecific taxa (Whang et al. 2002).

The taxonomic treatment and arguments developed herein are presented in a historical context beginning with André Michaux's *Flora Boreali-Americana* (1803) and relying heavily on the landmark treatment of *Amelanchier* by Karl Wiegand (1912).

METHODS

Study Site.—The Delmarva Peninsula comprises the eastern shore of Maryland, all of Delaware (New Castle, Kent and Sussex Counties) and the eastern shore of Virginia (Accomack and Northhampton Counties) bounded on the west by the Chesapeake Bay and the Susquehanna River and on the east by the Atlantic Ocean (Fig. 1). The Delmarva Peninsula lies south of the fall-line, a term used to describe the boundary between the Piedmont Province and the Atlantic Coastal Plain and falls entirely within the Outer Coastal Plain Mixed Forest Province of Bailey (1995). Elevations on the peninsula are mostly less than 20 m ASL and are underlain by relatively young Tertiary and Quaternary sediments of uniformly low relief (Schmidt 1993). It is mostly within the Oak-Pine forest region, with the northernmost counties transitional to the Oak-Chestnut region (Braun 1950). Significant habitat features include extensive fresh and salt tidal marshes, blackwater river swamps, barrier islands and Delmarva Bays (seasonal ponds). The climate of Delmarva is moderated by the Delaware Bay, Chesapeake Bay and the Atlantic Ocean and is characterized as having cool winters and warm, humid summers.

Character Selection and Sample Size Determination.—I used data from two characters: (1) length of the flowering inflorescence [hereafter abbreviated as Flinllen] and (2) length of the lowest pedicel on the flowering raceme [hereafter Flpedlen] as a model for determining sample size requirements in the field study. These two characters have been used by many authors (Ashe 1903; Jones 1946; Fernald 1941, 1950; Robertson 1974; Wiegand 1912, 1920) to describe *Amelanchier obovalis* and *A. canadensis* and were readily obtainable from herbarium sheets. I took measurements of Flinllen and Flpedlen from 54 accessions of both species from herbarium specimens borrowed from CM, DOV, FLAS, GA, MARY, NA, NCU, PH, US, USCH, VPI (acronyms follow Holmgren et al. 1990) and of personal collections from Delaware, Maryland, North Carolina and Virginia. Flpedlen had the lowest dispersion of scores ($\bar{u} = 11.88$ mm, $\sigma = 5.46$ mm, $N = 119$) and the ratio of the standard deviation to the mean, expressed as a percentage, (Coefficient of Variation) was 46%. Iterative sample size analysis (Sokal and Rohlf 1968, p. 247) converged on a sample size > 53 that would be sufficient for an 80% certainty of determining a 25% difference between means at the 5% significance level by Analysis of Variance. For the field study I chose an additional thirteen characters that I determined might be informative in describing variation in the complex: (1) the proportion of the length of the flowering inflorescence comprised by the lowest flowering pedicel [Flped_flinfl], (2) ovary pubescence during flowering [Flovpub], (3) flowering sepal position [Flsepos], (4) length of the fruiting inflorescence [Frinllen], (5) length of the lowest pedicel on the fruiting raceme [Frpedlen], (6) the proportion of the length of the fruiting inflorescence comprised by the lowest fruiting pedicel [Frped_frinfl], (7) ovary pubescence on the developing fruit [Frovpub], (8) sepal position on the developing fruit [Frsepos], (9) petal length [Petlen],

(10) petal width [Petwid], (11) the ratio of petal length/petal width [Petl_wratio], (12) the leaf length/width ratio [Lfl_wratio] and (13) the ratio of the widest point of the leaf relative to total leaf length [Lfwidpt]. Table 1 provides a complete list of characters, their descriptions and measurements. The means of five replicates per character on each individual were calculated and used in subsequent analyses for all quantitative characters. Of the total 15 characters, four were multi-state, categorical variables: flowering and fruiting sepal position [Flsepos, Frsepos] and flowering and fruiting ovary pubescence [Flovpub, Frovpub]; these characters are not included in analysis of variance but were collected for descriptive purposes and as a preliminary sample for future analysis.

Sampling.—During the late winter and early spring I marked 75 individuals of *Amelanchier* with permanent tags on a north-south transect from Cecil County, Maryland (39° 32' 38" N) to Northhampton County, Virginia (37° 08' 45" N). Additionally, I included a sample from within the core range of *Amelanchier obovalis* (Bladen County, North Carolina) matching the description of *Amelanchier obovalis* by Fernald (1950a) and Radford et al. (1968). I did not attempt to stratify the sample among disturbance levels, although in order to examine any correlations with disturbance and to avoid ecological bias in selecting the sample I marked individuals in both natural habitats (interior of swamp forests, hummocks along fresh-tidal rivers, pine flatwoods) and disturbed habitats (roadside verges, clearcuts, and powerlines). I returned to each marked individual during peak flower and mid-fruiting stages. I defined the peak flowering period as the stage when all flowers on the raceme had expanded and mature petals could be easily removed from the upper flowers. I defined the early fruiting stage as the period when the ovary on the developing fruit had swollen but the fruit was still green or just coloring and mature leaves were available.

Additional effort was made to examine variation in elongation of the lower pedicels over time, a character noted by several authors (Ashe 1903; Wiegand 1912; Fernald 1941; Jones 1946) and one that I thought might be informative for understanding the various taxonomic concepts of *Amelanchier obovalis* and *A. canadensis*. This additional character is not used in the multivariate analysis. I examined the difference between mean length of the lowest pedicel at peak flower and at mid-fruit by analysis of variance. Inflorescence and pedicel measurements were taken in the field, all other measurements were taken in the lab. All measurements utilized a digital caliper and an ocular micrometer scaled to tenths of a millimeter. Vouchers of flowering and fruiting material were collected from marked individuals at each site; these are deposited at the Maryland Department of Natural Resources Herbarium (Tawes), Annapolis, MD. Sampling began on 18 April 2005 and continued through 26 May 2005. Flowering, fruiting and leaf measurements were successfully gathered for 61 individuals.

Quantitative Morphological Analyses.—My overall objective for the analysis of quantitative morphological characters is to test the null hypothesis of no significantly distinguishable groups of individuals. To test the null hypothesis I looked for discrete clusters using Principal Components Analysis (PCA) based on the correlation matrix of eleven (Full dataset) and six (Type dataset) quantitative characters standardized by log transformation. I also used the Full dataset to reduce the dimensions of the dataset by eliminating highly correlated characters (Pearson's $r > 0.7$). Proportion of variance explained by each axis was compared with that expected under a broken-stick model (Jackson 1993). I plotted the first principal component against the second to graphically portray any relationships among individuals. Additionally, I created a second matrix from an

TABLE 1. List of the 15 character acronyms, their descriptions and measurement. All measurements taken to the nearest tenth of a millimeter.

Character acronym	Description and Measurement
Flinflen	Length of the flowering inflorescence at peak flower. Measured from the base of the distal-most flower on the raceme to point of insertion on the stem.
Flpedlen	Length of the lowest pedicel on the flowering raceme at peak flower. Measured from the base of the ovary to point of insertion on the raceme.
Flped_flinfl	Proportion of the length the flowering raceme comprised by the lowest pedicel.
Flovpub	Ovary pubescence on the terminal flower of the flowering raceme scored from 1 (glabrous) to 4 (densely tomentose).
Flsepos	Sepal position on the terminal flower of the flowering raceme scored along a scale from 1 (erect) to 4 (tightly reflexed) in comparison to an imaginary transverse plane through the ovary.
Frinflen	Length of the fruiting inflorescence. Measured from the base of the distal-most fruit on the raceme to point of insertion on the stem.
Frpedlen	Length of the lowest pedicel on the fruiting raceme at mid-fruit. Measured from the base of the ovary to point of insertion on the raceme.
Frped_frinfl	Proportion of the length of the fruiting raceme comprised by the lowest pedicel.
Frovpub	Ovary pubescence on the terminal fruit of the fruiting raceme scored along a scale from 1 (glabrous) to 4 (densely tomentose).
Frsepos	Sepal position on the terminal fruit of the fruiting raceme scored along a scale from 1 (erect) to 4 (tightly reflexed) in comparison to an imaginary transverse plane through the ovary.
Petlen	Length of mature, expanded petals measured from distal-most point to insertion on the hypanthium.
Petwid	Width of mature expanded petals measured at the widest point.
Petl_wratio	Ratio of petal length/petal width.
Lfl_wratio	Ratio of leaf length/leaf width.
Lfwidpt	Ratio of the widest point along the leaf axis (measured from base)/total leaf length.

agglomerative, hierarchical Cluster Analysis using Euclidean distance and Ward's method of linkage (McCune & Grace 2002). This second matrix was used as an overlay on the PCA scatterplot to assist in visualizing groups. PCA and Clustering were performed on Pcord version 4.14 (McCune & Mefford 1999).

A separate objective was to determine the identity (group membership) of the type specimen of *Amelanchier obovalis* in multivariate character space. I performed both PCA and Clustering based on the correlation matrix of six quantitative characters derived from analysis of the Full dataset and that were also obtainable from the type specimen: Petlen, Flinflen, Flpedlen, Flped_flinfl, Lfl_wratio, and Lfwidpt. The Type dataset was organized into a group by character matrix and exported to SAS version 9.1 (SAS Institute, Cary, NC, USA) for Multivariate Analysis of Variance (MANOVA, GLM procedure). MANOVA tests for an overall multivariate effect of the group model and performs pairwise comparisons between character means (mean vectors) for all groups for each character. Approximate univariate normality of morphometric characters within each group was assessed by inspection of frequency histograms, accepting normality with skewness < 1 (McCune & Grace 2002). MANOVA is robust to multivariate non-normality and Levene's test was used to ascertain homogeneity of variances within each group. MANOVA is used to test the null hypothesis of no significant differences between the mean vectors of each group.

Assessment of Taxonomic Rank.—I utilize the concepts of genetic and ecological exchangeability introduced by Crandall et al. (2000) to assess population distinctiveness and extend that method to assessing taxonomic rank. Species populations are genetically exchangeable if there is evidence of ample gene flow between them. Ecological exchangeability is demonstrated if individuals can be moved between populations and can occupy the same ecological niche. Exchangeability is viewed from both recent and historical perspectives, e.g., two taxa may currently experience gene flow due to breakdown of intrinsic or extrinsic barriers via anthropogenic causes but the populations may have historically experienced (e.g., presettlement) little gene flow.

RESULTS

Full Dataset.—Eigenvalues for the first two axes, representing 56% of the total variation, exceeded their broken-stick values and were chosen for interpretation (Table 2). PCA-1 comprises > 37% of the variance in the dataset. Five morphological characters ordinate individuals along PCA-1. These are, in descending order in the loading matrix (Table 3): Flpedlen, Frpedlen, Frinflen, Flinflen and Petlen. PCA-1 is thus a size axis. PCA-2 comprises > 19% of the variance in the dataset. Five morphological characters ordinate individuals along PCA-2. These are, in descending order in the loading matrix (Table 3): Flped_flinfl, Frped_frinfl, Lfl_wratio, Flinflen and Frinflen. PCA-2 is chiefly a shape axis. The characters most highly correlated with both PCA axes are also very highly correlated with each other, in particular, flowering and fruiting stages of the inflorescence are redundant (Table 4). Flowering characters were selected for the final matrix.

Type Dataset.—Six characters were used in the analysis of the Type dataset: Petlen, Flinflen, Flpedlen, Flped_flinfl, Lfl_Wratio and Lfwidpt. These six quantitative characters were obtainable from the type specimen of *Amelanchier obovalis* and serendipitously mirrored the set of minimally correlated characters derived from analysis of the Full dataset with the exception of Flpedlen ($r = 0.708$), which I maintained because of its use as an informative character in most treatments. The dendrogram produced by Cluster Analysis (Fig. 2) is scaled by an objective function that measures the loss of information at each step; as groups are fused the amount of information decreases until all groups are fused and no information remains (McCune & Grace 2002). In the iterative process, five and higher order groups were composed of single (outlier) individuals and selection of three groups combined groups 2 and 3 into a single membership cluster. I chose to overlay a four-group cluster on the PCA as this appeared to be the maximum number of well-supported groups (e.g., long branches of the dendrogram) and corresponded to my field observations of the number of putative morphological forms prior to sampling and roughly to the different habitat types that were sampled (e.g., tidal and nontidal swamps, low Pine woodlands, and sand ridges). The PCA scatterplot with Cluster overlay (Fig. 3) shows a single distinct cluster at the far left of PCA-1 and central to PCA-2. The eigenvalues for the first two principal components, representing >65% of the total variation, were selected for interpretation; however, only the second axis exceeded its broken-stick value (Table 5). PCA-1 comprises > 39% of the variance in this dataset. Three morphological characters ordinate individuals along PCA-1. These are, in descending order in the loading matrix (Table 6): Flpedlen, Flinflen and Petlen. PCA-1 is a size axis clearly separating group 1 (positive affinities) and group 4 (negative affinities) but with overlap between groups 2 and 3 at the origin. PCA-2 comprises > 26% of the variance in the dataset. Three characters ordinate individuals along PCA-2. These are, in

TABLE 2. **Full dataset.** Eigenvalues, percent variance extracted and broken-stick comparison of four Principal Component axes with eigenvalues > 1.

Axis	Eigenvalue	Percent of variance	Cumulative Percent	Broken-stick Eigenvalue
1	4.106	37.325	37.325	3.020
2	2.112	19.204	56.529	2.020
3	1.482	13.470	69.999	1.520
4	1.199	10.902	80.901	1.187

TABLE 3. **Full dataset.** Principal components loading matrix of the correlations between eleven morphological characters and component scores (eigenvectors). The five highest correlations with the eigenvector are in bold type.

Character	Eigenvector	
	1	2
Petlen	-0.3267	0.0632
Petwid	-0.2567	0.0249
Petl_wratio	-0.0921	0.0471
Flinflen	-0.3826	-0.3641
Flpedlen	-0.4620	0.0131
Flpedl_flinfl	-0.2524	0.4800
LfL_wratio	0.0045	-0.4525
Lfwidpt	0.0434	0.3073
Frinflen	-0.3906	-0.3242
Frpedlen	-0.4433	0.0426
Frpedl_frinfl	-0.2107	0.4732

descending order in the loading matrix (Table 6): Lfl_wratio, Flped_flinfl and Lfwidpt. PCA-2 is a shape axis that most clearly separates group 3 (positive affinities) from group 2 (negative affinities).

The type specimen of *Amelanchier obovalis* is nested near the center of group 1 outside of the range of variation (along PCA-1) in other groups (see Fig. 3). Descriptive statistical analysis of the four-group model, calculating the means, standard deviations and 90% confidence intervals of morphological characters most highly correlated with PCA-1 and PCA-2 provide some morphological coherence of the groups with strong positive or negative affinities along the principal component axes (Table 7). Group 1 (triangles) consists of individuals (on PCA-1) having short petals (6.8 ± 0.9 mm), short flowering inflorescences (28.7 ± 0.9 mm), and short lower pedicels (7.9 ± 1.3 mm). On the second PCA axis group 1 consists of individuals with leaves averaging 1.8 times as long as wide (1.79 ± 0.22) that are widest above the midpoint (0.548 ± 0.037) and have more or less cylindrical inflorescences (0.283 ± 0.053). Group 4 (stars) consists of individuals (on PCA-1) having long petals (8.8 ± 1.2 mm), long flowering inflorescences (47.8 ± 3.9 mm) and long lower pedicels (15.8 ± 1.7 mm). On the second PCA axis group 4 consists of individuals with leaves averaging 1.8 times as long as wide (1.80 ± 0.18), that are widest near the midpoint (0.519 ± 0.034), and have spreading inflorescences (0.335 ± 0.042). Group 2

TABLE 4. **Full dataset.** Cross-products matrix of Pearson's Correlation Coefficients (r) for eleven morphological characters. Values of $r \geq 0.7$ (rounded) are in bold type.

	Petlen	Petwid	Petl_wratio	Flinflen	Flpedlen	Flpedl_flinfl	Lfl_wratio	Lfwidpt	Frinflen	Frpedlen	Frpedl_frinfl
Petlen	1	0.669	0.396	0.368	0.497	0.327	0.005	0.137	0.385	0.398	0.156
Petwid	-	1	-0.410	0.328	0.356	0.163	-0.049	0.164	0.314	0.326	0.118
Petl_wratio	-	-	1	0.062	0.185	0.202	0.043	-0.057	0.104	0.107	0.057
Flinflen	-	-	-	1	0.778	-0.018	0.229	-0.271	0.839	0.652	-0.021
Flpedlen	-	-	-	-	1	0.612	-0.024	-0.117	0.708	0.794	0.372
Flpedl_flinfl	-	-	-	-	-	1	-0.329	0.146	0.058	0.434	0.616
Lfl_wratio	-	-	-	-	-	-	1	-0.168	0.192	-0.039	-0.311
Lfwidpt	-	-	-	-	-	-	-	1	-0.179	-0.094	0.073
Frinflen	-	-	-	-	-	-	-	-	1	0.759	-0.042
Frpedlen	-	-	-	-	-	-	-	-	-	1	0.602
Frpedl_frinfl	-	-	-	-	-	-	-	-	-	-	1

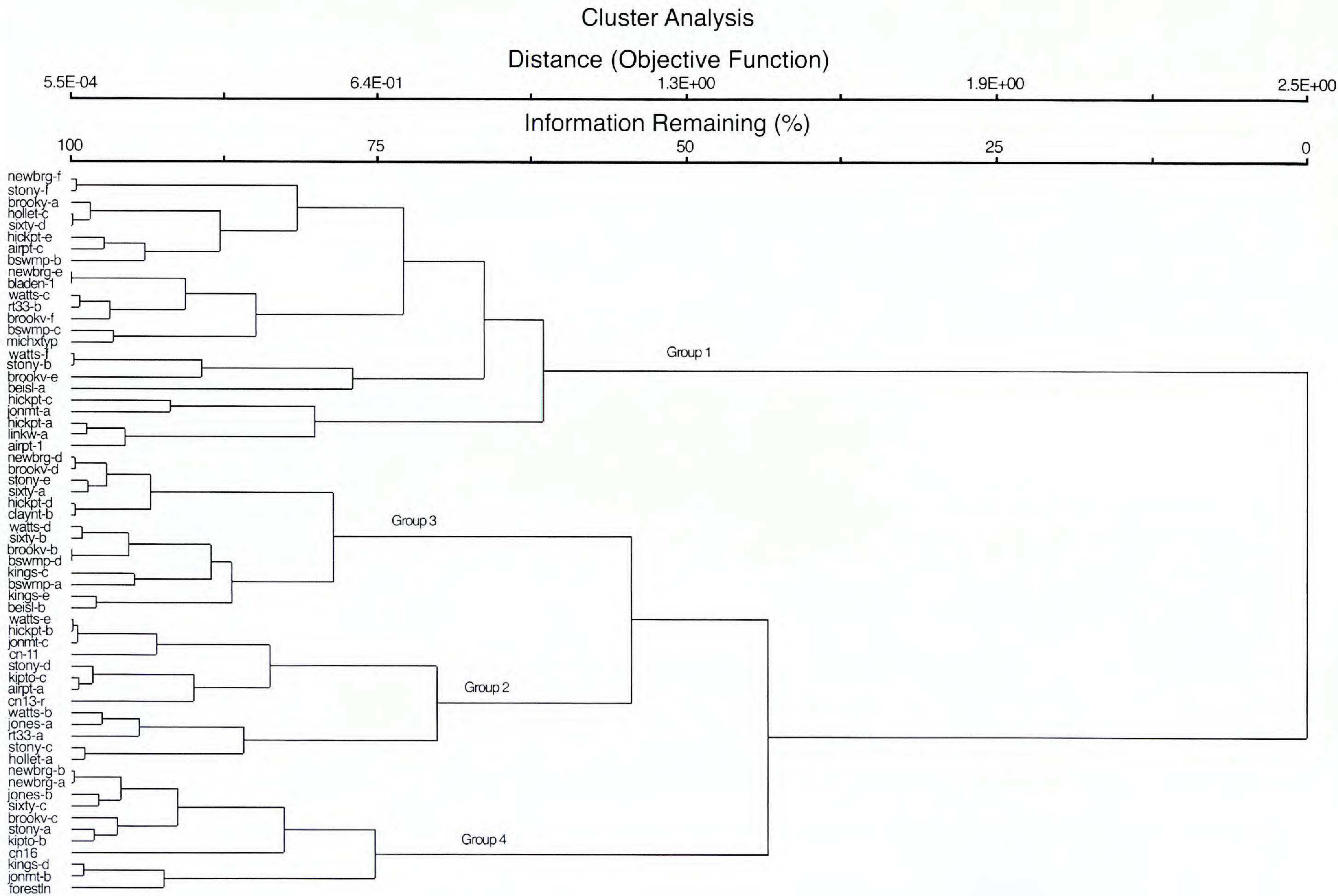


Fig. 2. Dendrogram produced by Cluster Analysis showing pruning points and group assignments of 62 individuals.

Principal Components Analysis

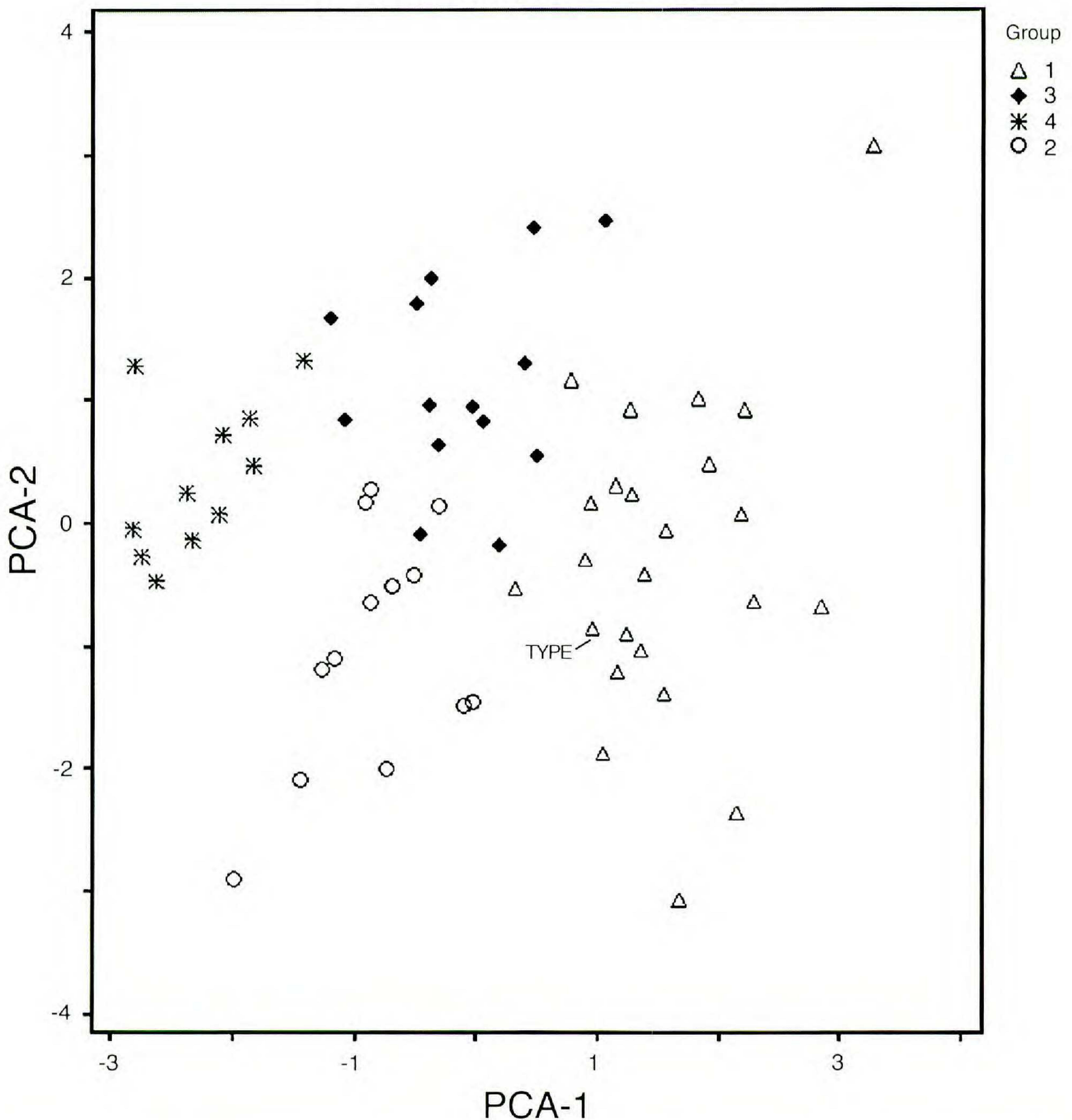


FIG. 3. PCA scatterplot with Cluster overlay. Symbols denote group membership: triangles = group 1, circles = group 2, diamonds = group 3, stars = group 4. Type specimen of *Amelanchier obovalis* indicated.

(circles) consists of individuals (on PCA-1) having intermediate petal lengths (7.7 ± 0.8 mm), flowering inflorescences (35.1 ± 4.6) and lower pedicels (12.6 ± 1.7 mm). On the second PCA axis group 2 consists of individuals with leaves averaging 1.7 times as long as wide (1.67 ± 0.14) that are widest above the midpoint (0.547 ± 0.057) and have widely spreading flowering inflorescences (0.363 ± 0.043). Group three (diamonds) consists of individuals (on PCA-1) having intermediate length petals (7.3 ± 0.9 mm), long flowering inflorescences (39.6 ± 3.0 mm) with short lower pedicels (10.8 ± 1.1 mm). On the second PCA axis group 3 consists of individuals with leaves averaging 1.9 times as long as wide (1.87 ± 0.17), that are widest at the midpoint (0.503 ± 0.029), and have cylindrical flowering inflorescences (0.272 ± 0.026).

TABLE 5. **Type dataset.** Eigenvalues, percent variance extracted and broken-stick comparison of two Principal Component axes with eigenvalues > 1.

Axis	Eigenvalue	Percent of variance	Cumulative Percent	Broken-stick Eigenvalue
1	2.345	39.082	39.082	2.450
2	1.575	26.243	65.325	1.450

TABLE 6. **Type dataset.** Principal Components loading matrix of the correlations between six morphological characters and component scores (eigenvectors). The three highest correlations with the eigenvector are in bold type.

Character	Eigenvector	
	1	2
Petlen	-0.4524	-0.1036
Flinflen	-0.4994	0.4079
Flpedlen	-0.6326	0.0032
Flpedl_flinfl	-0.3720	-0.5164
LfL_wratio	0.0144	0.5610
Lfwidpt	0.0842	-0.4914

Multivariate Analysis of Variance.—There is a significant overall multivariate effect of the four-group model (Table 8) and significant F ratios were found for five of the six quantitative characters (Table 9). Pair-wise comparisons between all groups (Table 9) determined significant differences between all pairwise group mean vectors for Flinflen and five of six comparisons for Flpedlen. Petlen was significant for 4 of 6 group comparisons, Flped_flinfl was significant in 4 of 6 group comparisons, and Lfwidpt was significant for 2 of 6 group comparisons. Differences between group mean vectors for LfL_Wratio were not significant. Group 4 contains the most distinctive individuals, as expressed by all pairwise comparisons of mean vectors for Petlen, Flinflen, and Flpedlen and two of three pairwise comparisons for Flped_flinfl. Group 1 is also distinctive as expressed by all group comparisons for Flinflen and Flpedlen, 2 of 3 pairwise comparisons for Petlen, 2 of 3 pairwise comparisons for Flped_flinfl, and 1 of 3 pairwise comparisons for Lfwidpt. Group 2 is significant in all pairwise comparisons for Flinflen, 2 of 3 comparisons of Flpedlen, 2 of 3 pairwise comparisons for Petlen, 2 of 3 pairwise comparisons for Flped_flinfl, and 1 of 3 pairwise comparisons for Lfwidpt. Group 3 is significant in all pairwise comparisons for Flinflen, 2 of 3 comparisons of Flpedlen, but only 1 of 3 pairwise comparisons for Petlen, 2 of 3 comparisons for Flped_flinfl and 2 of 3 comparisons for Lfwidpt.

The presence of a large sample of individuals with intermediate phenotypes suggests ample gene flow (genetic exchangeability) between the groups. Ecological exchangeability is demonstrated by the occurrence of morphologically distinct individuals occurring within the same habitat type.

Taxonomic Usefulness of the Elongation of the Lowest Pedicel.—There is significant variation among groups in the elongation of the lowest pedicel from peak flowering to mid-fruiting as determined by Analysis of Variance. The difference between the mean

TABLE 7. Descriptive statistics of six characters most highly correlated with the principal components (PCA-1 and PCA-2) under a four-group model. Columns under Group labels are: N = number of individuals in group, means \pm standard deviations, (ranges), [minimum; maximum], {90% Confidence Intervals}. All measurements reflect raw (untransformed) scores.

Character	Group 1	Group 2	Group 3	Group 4
	N = 24	N = 13	N = 14	N = 11
Petlen	6.8 \pm 0.9 (3.0) [5.6; 8.6] {6.5—7.1}	7.7 \pm 0.8 (3.5) [5.9; 9.4] {7.3—8.1}	7.3 \pm 0.9 (3.0) [5.8; 8.8] {6.9—7.7}	8.8 \pm 1.2 (4.0) [6.5; 10.5] {8.1—9.5}
Flinflen	28.7 \pm 0.9 (17.3) [18.7; 36.0] {27.1—30.3}	35.1 \pm 4.6 (14.4) [28.4; 42.8] {32.8—37.4}	39.6 \pm 3.0 (8.8) [35.0; 43.8] {38.2—41.0}	47.8 \pm 3.9 (10.6) [42.2; 52.8] {45.7—49.9}
Flpedlen	7.9 \pm 1.3 (5.7) [5.6; 11.3] {7.4—8.4}	12.6 \pm 1.7 (5.6) [9.6; 15.2] {11.8—13.4}	10.8 \pm 1.1 (3.4) [9.3; 12.7] {10.3—11.3}	15.8 \pm 1.7 (5.2) [13.2; 18.4] {14.9—16.7}
Flpedl_flinfl	0.283 \pm 0.053 (0.238) [0.167; 0.405] {0.264—0.302}	0.363 \pm 0.043 (0.163) [0.293; 0.456] {0.342—0.384}	0.272 \pm 0.026 (0.108) [0.212; 0.320] {0.260—0.284}	0.355 \pm 0.042 (0.123) [0.273; 0.396] {0.332—0.378}
LfL_wratio	1.79 \pm 0.22 (0.70) [1.47; 2.17] {1.71—1.87}	1.67 \pm 0.14 (0.45) [1.41; 1.86] {1.60—1.74}	1.88 \pm 0.17 (0.58) [1.64; 2.22] {1.80—1.96}	1.80 \pm 0.18 (0.59) [1.56; 2.15] {1.70—1.90}
Lfwidpt	0.548 \pm 0.037 (0.145) [0.471; 0.616] {0.535—0.561}	0.547 \pm 0.057 (0.171) [0.441; 0.612] {0.522—0.572}	0.503 \pm 0.029 (0.114) [0.468; 0.582] {0.490—0.516}	0.519 \pm 0.034 (0.097) [0.473; 0.570] {0.500—0.538}

flowering pedicel length and mean fruiting length are not significant in group 4 ($P = 0.15$, $F_{\alpha .05 [1,20]} = 2.23$, $F_{critical} = 4.35$) indicating that the inflorescence elongates very little from peak flower to mid-fruit. Significant differences between mean flowering and mean fruiting pedicel length were found in the other three groups. Group 1 has the largest F ratio ($P < .0001$, $F_{\alpha .05 [1,44]} = 26.39$, $F_{critical} = 4.06$) indicating that the lowest pedicel elongates significantly from peak flower to fruit. Group 2 and group 3 also show significant differences in this character (Group 2: $P = .001$, $F_{\alpha .05 [1,24]} = 13.53$, $F_{critical} = 4.26$; Group 3: $P = .0006$, $F_{\alpha .05 [1,26]} = 15.17$, $F_{critical} = 4.23$).

DISCUSSION

Multivariate analysis of morphological characters distinguishes four groups of specimens within the *Amelanchier* complex on the Delmarva Peninsula. Group 1 contains shrubby or multi-stemmed *Amelanchier* with short and rather fat petals, short, cylindrical flowering and fruiting inflorescences with short lower pedicels. This group of specimens is referable to *Amelanchier obovalis*; the type specimen nests within this group outside of the range of variation of other groups. This group may be more clearly visually defined by

TABLE 8. MANOVA test criteria and F approximations for the hypothesis of no overall effect of the four-group model.

Statistic	Value	F Value	Num DF	Den DF	Pr . F
Wilk's Lambda	0.04823940	14.12	18	150.39	,.0001
Pillai's Trace	1.47957567	7.29	18	165	,.0001
Hotelling-Lawley	9.83905376	27.18	18	100.15	,.0001

TABLE 9. Univariate F values (GLM procedure) and $P > F$ for six informative characters and pairwise group comparisons of character means using Tukey's Studentized Range (HSD). Critical value of Studentized Range = 3.74. * = Comparisons significant at $\alpha = .05$, $df = 58$; ns = not significant. Grp1 = *A. obovalis*; Grp4 = *A. canadensis*.

Character	F ratio for Character	P . F	Group Comparison (Tukey)	Difference b/w means	Confidence Limits 95%	
Flinflen	61.59	0.0001	grp4-grp2	13.19	8.82—17.56	*
			grp4-grp3	8.25	3.95—12.55	*
			grp4-grp1	19.10	15.21—22.98	*
			grp2-grp3	4.98	0.827—9.05	*
			grp2-grp1	5.91	2.32—9.58	*
			grp3-grp1	10.85	7.26—14.43	*
Flpeden	68.86	,0.0001	grp4-grp2	3.70	2.01—5.39	*
			grp4-grp3	5.05	3.39—6.72	*
			grp4-grp1	7.93	6.42—9.43	*
			grp2-grp3	1.35	-0.24—2.94	ns
			grp2-grp1	4.22	2.80—5.64	*
			grp3-grp1	2.87	1.48—4.26	*
Flped_flinfl	10.16	,0.0001	grp4-grp2	0.019	-0.032—0.070	ns
			grp4-grp3	0.063	0.012—0.113	*
			grp4-grp1	0.053	0.007—0.098	*
			grp2-grp3	0.081	0.033—0.129	*
			grp2-grp1	0.071	0.028—0.114	*
			grp3-grp1	0.010	-0.032—0.052	ns
Lfl_wratio	2.01	0.1228	grp4-grp2	0.104	-0.106—0.314	ns
			grp4-grp3	0.079	-0.127—0.285	ns
			grp4-grp1	0.016	-0.171—0.203	ns
			grp2-grp3	0.183	-0.015—0.380	ns
			grp2-grp1	0.088	-0.089—0.264	ns
			grp3-grp1	0.094	-0.078—0.267	ns
Lfwidpt	5.99	0.0013	grp4-grp2	0.031	-0.009—0.072	ns
			grp4-grp-3	0.017	-0.023—0.057	ns
			grp4-grp1	0.030	-0.006—0.066	ns
			grp2-grp3	0.048	0.010—0.086	*
			grp2-grp1	0.002	-0.033—0.036	ns
			grp3-grp1	0.046	0.013—0.080	*
Petlen	12.13	0.0001	grp4-grp2	1.11	0.079—2.15	*
			grp4-grp3	1.53	0.510—2.55	*
			grp4-grp1	2.06	1.14—2.98	*
			grp2-grp3	0.41	-0.559—1.39	ns
			grp2-grp1	0.94	0.073—1.81	*
			grp3-grp1	0.53	-0.320—1.38	ns

eliminating outliers; however, eliminating these individuals in the PCA does not change group membership and these specimens do appear to represent natural variation within the group. One individual classified in group 1 (upper right corner of Fig. 3) deviates from the morphological group defined here by an extremely narrow cylindrical inflorescence. This individual may best be recognized as a separate entity; however, no other similar individual or specimen was located during sampling. Individuals forming group 1 (*A. obovalis*) were collected chiefly from sandy woodlands and barrens but did occur on hummocks along tidal creeks and thicket margins around non-tidal wetlands in disturbed and in nearly pristine habitats. Individuals are typically low and shrubby but may grow to several meters in absence of disturbance; this was ideally illustrated by single, apparently clonal individuals with stems that were inside and outside of a roadside-mowing regime.

Group 4 corresponds to a group of tall, arborescent or multi-stemmed *Amelanchier* with large petals and long lower pedicels forming long, widely spreading flowering and fruiting inflorescences. This group of specimens is referable to *Amelanchier canadensis*, matching as well as can be expected the type specimen and at least part of the historical circumscriptions. Individuals in group 4 (*A. canadensis*) were collected from both tidal and non-tidal swamp forests and were easily distinguished in the field. This species occurs sympatrically with *Amelanchier obovalis* in some habitats.

Group 1 and group 4 correspond to known taxonomic entities (*Amelanchier obovalis* and *A. canadensis* respectively) but group 2 and group 3, despite the statistical significance of several pairwise comparisons of character mean vectors in the MANOVA could not be assigned to distinctive forms such as might arise as microspecies. I hypothesize that group 2 and group 3 are members of an agamic complex derived from hybridization between *Amelanchier canadensis* and *A. obovalis*. Evidence of apomixis has been demonstrated in *Amelanchier canadensis* (Campbell et al. 1987) but not in *A. obovalis*. However, evidence to support this hypothesis may be drawn from my statistical analysis and observation. First, both *Amelanchier canadensis* and *A. obovalis* (as clear entities) were observed to occur within the same habitat patch in the study area and were observed to have overlapping phenologies, which increase the probabilities that natural hybridization occurs. Second, the means of important classification characters in group 2 and group 3 (with 90% confidence intervals) consistently occupy ranges intermediate between *Amelanchier canadensis* and *A. obovalis* (Table 7). Finally, the members of groups 2 and 3 appear morphologically heterogeneous and do not correspond to the four putative morphological forms that I noted in the field prior to sampling or to a particular habitat type. My field observations were that one form was referable to *Amelanchier obovalis* (group 1), a second to *Amelanchier canadensis* (group 4), a third group comprised the pubescent-ovary forms within group 1 and the fourth, an early flowering *Amelanchier* with small petals on hummocks along tidal creeks I now believe are consistent with *Amelanchier obovalis*.

Additionally, the discrimination of multivariate character space held by group 2 versus group 3 is uncertain. Group 2 and 3 separate nearly at the origin of PCA-2 (Fig. 3) and the character most highly correlated with this second axis ($r = .704$) is Lfl_Wratio, a character that fails statistical significance tests between groups in Analysis of Variance (see Table 9). Further, comparison of mean vectors of two important characters (Flpedlen and Petlen) between group 2 and group 3 are not significant (Table 9). Finally, the iterations of Cluster Analysis join group 2 and 3 in a three-group model and then collapse into group 4 (*A. canadensis*) in a two-group model. If I accept more variation in *Amelanchier canadensis* and consider a two-group model composed of *Amelanchier*

obovalis and a new group containing all the members of groups 2, 3 and 4 then my performance in keying vouchers would certainly improve but accepting this variation comes with a heuristic cost in that I obscure the only spatially distinctive cluster resulting from PCA. Given the well-documented propensity for hybridization and the formation of agamic complexes in *Amelanchier*, the most reasonable assumption is that individuals within group 2 and group 3 do constitute intermediate forms due to incomplete reproductive isolation between *Amelanchier canadensis* and *A. obovalis*.

I conclude that the multivariate character space occupied by *Amelanchier obovalis* exhibits significant phenetic dissimilarities with the other groups as expressed by its distinctiveness in Cluster Analysis (e.g., the long branch before joining) and by statistical significance of the majorities of group comparisons of character mean vectors for Flinllen, Flpedlen, Petlen, and Flped_flinfl. The discreteness of multivariate character space occupied by *Amelanchier canadensis* can be determined both visually (occurrence of a distinct cluster in the PCA) but also by the statistical significance of the majorities of group comparisons of character mean vectors for Flinllen, Flpedlen, Petlen and Flped_flinfl. However, the presence of numerous intermediate specimens violates most commonly accepted taxonomic conceptions of species status. Subspecies as a taxonomic rank is poorly defined in the literature of taxonomic botany and is used more or less interchangeably with variety (McDade 1995; Nesom and Lipscomb 2005). Wiegand (1912), Fernald (1950a) and Jones (1946) assigned the rank of variety to those distinctive forms of *Amelanchier* that occupied a particular geographical area and/or had a habitat preference slightly different than that typical of the species. Campbell and Dickinson (1990) concluded that nonconcordance between morphological and breeding units in Maloid apomicts rendered the biological species concept inappropriate and that a morphospecies concept may be necessary to deal with evolutionary complexity in the Maloideae. In this study I found no well-defined geographical or ecological separation between the taxa. However, I must also consider that the high frequency of intermediate forms found in the study area may reflect the long disturbance history of the Delmarva Peninsula and this disturbance history is responsible for recent, but perhaps not historical, genetic and ecological exchangeability (Crandall et al. 2000). That the frequency of disturbance often correlates with the number of hybrids and 'perplexing forms' has been the subject of repeated observation and much discussion among authors since Wiegand (1912). The study populations of *Amelanchier* fall under Crandall's et al. (2000) case of "anthropogenic convergence on demographic exchangeability" where we continue to treat the populations as distinct units but not as distinct species. Both taxa are distinctive enough morphologically and intermediate forms may not occur with such frequency in other regions. In the taxonomic treatment below, I utilize the taxonomic concept of "variety" defined as the primary taxonomic level below species (International Code of Botanical Nomenclature, 4.1).

TAXONOMIC TREATMENT

***Amelanchier canadensis* (L.) Medic. var *obovalis* Michx.** TYPE: *Mespilus canadensis* var. *obovalis* Michx., Fl. Bor. Amer. 1:291. 1803. *Amelanchier obovalis* (Michx.) Ashe, Bot. Gaz. 35:434. 1903, in part. *Amelanchier obovalis* (Michx.) Ashe, M.L. Fernald in *Rhodora* 43:566. 1941, in part. *Amelanchier oblongifolia* (Torr. & A. Gray) Roemer, K.M. Wiegand in *Rhodora* 14:147-150. 1912, in part. *Amelanchier canadensis* ssp. *obovalis*, P. Landry, Bull. Soc. Bot. Fr. 122:248. 1975.

Amelanchier obovalis is a rather enigmatic species with a long history of circumscription problems. André Michaux (1803) described *Mespilus canadensis* var. *obovalis* from

“carolina inferiore” (lower Carolina) as “humilior; folius oblongiscule obovalibus” (low with oblong obovate leaves) and “arbriss de deux pieds haut” (a shrub about two feet tall). The Michaux specimen (P) is very well preserved having several stems with inflorescences and petals intact and a single stem with (apparently mature) expanded leaves. A century later Ashe (1903) created a new combination, *Amelanchier obovalis* (Michx.) Ashe describing a shrub of “swamps and loose soils” 9–15 dm tall or a small tree to four meters tall with flowering inflorescences 3–5 cm long, the lowest pedicels 3–9 mm but becoming elongate (2–3 cm) in fruit. Wiegand (1912), probably the most influential of *Amelanchier* taxonomists, includes *Amelanchier obovalis* (Michx.) Ashe under his “fastigate not stoloniferous” *Amelanchier oblongifolia* (Torr. & A. Gray) Roemer, stating that it “seemed to be this species” but it is not clear that Wiegand ever saw any of Ashe’s collections from the southeastern United States. Wiegand (1912) described his *A. oblongifolia* as a shrub with slender upright stems in rather dense fastigate clumps with inflorescences 2.5–6 cm long, the lowest pedicels 8–18 mm long but scarcely longer in fruit. M.L. Fernald (1941), after several field seasons exploring the Pine Barrens of southeastern Virginia, disagreed with Ashe’s description of *Amelanchier obovalis*, particularly regarding plant height, and subsequently ignored his treatment, describing *Amelanchier obovalis* (Michx.) Ashe as a “dwarf and stoloniferous” shrub with flowering inflorescences 1–2.5 cm long with lower pedicels lengthening only to 3–8 mm. Fernald (1950a) distinguished the species in his key chiefly by plant habit in a major couplet: “stoloniferous or surculose loosely colonial shrubs” 0.2–2 M. high (*A. obovalis*); versus “fastigate coarse and tall shrubs or arborescent” (*A. canadensis*). Jones (1946) closely followed Fernald’s (1941) treatment of *Amelanchier obovalis* as “low shrubs, surculose, forming loose colonies” but with flowering inflorescences 1–3 cm long with lower pedicels 1–3 mm, becoming 3–8 (11–14 mm) long in fruit. Landry (1975) describes *Amelanchier obovalis* as a subspecies of *A. canadensis* with the major difference between the two subspecies being the general size of floral inflorescences and (very vaguely) the length of the lowest pedicels with *Amelanchier canadensis* ssp. *canadensis* having “rather large” flower clusters and lower pedicels at least 6 mm long versus clusters of flowers small and lower pedicels more than 6 mm long (*A. canadensis* ssp. *obovalis*).

The members of Group 1 (*Amelanchier canadensis* var. *obovalis*) are both low shrubs with apparent vegetative spread and tall, slender, multi-stemmed shrubs that occurred in a variety of habitats including hummocks on margins of tidal creeks and rivers, sandy pine forests and barrens, roadsides and under powerlines. In both flowering and fruiting stages the lowest pedicels were the shortest in the dataset and although they did elongate in fruit the extremes that Ashe (1903) suggested (10–20 mm) were not observed. I suspect that Ashe, perhaps due to finding very similar phenotypes in a variety of habitats or by witnessing the same complex as analyzed herein conflated the characteristics of both taxa. M.L. Fernald (1941), on the other hand, accepted only the extreme shrubby forms of the species and somewhat idiosyncratically noted that the taller species was probably *Amelanchier austromontana*, a species that Ashe (1918) described from the Southern Appalachian Mountains and not the southern Coastal Plain.

***Amelanchier canadensis* (L.) Medic. var. *canadensis*.** TYPE: *Mespilus canadensis* L., Sp. Pl. 1:498. 1753.

Amelanchier oblongifolia (Torr. & A. Gray) Roemer, K. Wiegand in *Rhodora* 14:147–150. 1912, in part.

Amelanchier obovalis (Michx.) Ashe, Bot. Gaz. 35:434. 1903, in part.

Amelanchier canadensis (L.) Medic. is the earliest combination in *Amelanchier*; the type

specimen (LINN) from "habitat in Virginia, Canada" contains a single stem with five leaves and the remnants of a fruiting inflorescence with three fruit. The type is of limited usefulness as the characters used by major authors of the genus to separate *Amelanchier canadensis* from *A. obovalis*, e.g. plant habit, petal length, flowering inflorescence length and lowest pedicel length are absent. Wiegand's (1912) circumscription of *Amelanchier oblongifolia* appears to include both *Amelanchier canadensis* and *A. obovalis* as the ranges of character measurements are inclusive of both taxa. Similarly, Ashe's (1903) circumscription of *Amelanchier obovalis* appears to include characteristics of both species. It is very difficult to generalize but overall most authors treat *Amelanchier canadensis* as a fastigate shrub forming alder-like clumps having larger petals, and larger inflorescences than the low, shrubby and stoloniferous *Amelanchier canadensis* var. *obovalis*.

The members of Group 4 (*Amelanchier canadensis* var. *canadensis*) comprise a group of tall, fastigate shrubs and small trees having the largest petal dimensions, very long flowering and fruiting inflorescences with long lower pedicels forming widely spreading inflorescences. This variety is easily distinguished in the field however numerous individuals with characters intermediate between the two varieties are present in the study area. Individuals of *Amelanchier canadensis* var. *canadensis* were located, mostly, in natural habitats associated with tidal and non-tidal wetlands, however, there appears to be little habitat specificity and these individuals occurred often in close proximity to var. *obovalis*. Wiegand's notion that the pedicels of his *Amelanchier oblongifolia* are "scarcely longer in fruit" appears consistent with the results of Analysis of Variance comparing lowest pedicel lengths in flowering versus fruiting material; although, it is apparent that Wiegand also conflated the characteristics of both taxa, perhaps because he was unfamiliar with the more southern forms constituting *Amelanchier obovalis*.

KEY

The following key to *Amelanchier canadensis* includes the other common species occurring in the study area, *Amelanchier arborea* (Michx. f.) Fernald. In keying *Amelanchier* one should realize that many specimens would not key confidently without observations (collections) made throughout the growing season. Those specimens with intermediate characters are likely part of the species complex and so should be simply identified as 'comparing favorably' with one variety or the other. The twenty-four members of group 1 (*A. c. obovalis*) provide the mean and range (one standard deviation) of characters that should be used to identify this species and the eleven members of group 4 (*A. c. canadensis*) provide the mean and range of the same morphological characters.

Specimens with entire leaves from the southeastern Coastal Plain may constitute var. *subintegra* Fernald but this putative taxon is not included in the key as its evaluation was not within the scope of this manuscript.

Sepals in flower and in fruit tightly recurved and appressed to the ovary, leaves subcordate at base, acute to acuminate at the apex and coarsely serrate. Arborescent species of upland woods

_____ **Amelanchier arborea**

Sepals in flower and in fruit not tightly appressed to ovary, leaves rounded at base, rounded to broadly rounded at apex and finely serrate. Tall shrubs with slender stems or dwarf shrubs with evident vegetative spread, chiefly of swamps and barrens at low elevations

___ **Amelanchier canadensis**

Petals (5.9–)6.8(–7.7) mm long and (2.6–)3.1(–3.6) mm wide, inflorescences at peak flower (27.8–)28.7(–29.6) mm, elongating in fruit to (27.2–)32.1(–37.1) mm, lowest pedicels (flowering) (6.6–)7.9(–9.2) mm, elongating in fruit to (8.2–)11.0(–13.8) mm. Inflorescences usually cylindrical, the lowest pedicel averaging 28% of the total inflorescence length at flowering, and 35% percent

in fruit. Leaves on older branches chiefly obovate, the widest point occurring at 51–58 percent of the total leaf length. Sepals usually erect in flower, but often spreading during maturation of the ovary. Ovary summit usually glabrous but a variable amount of pubescence occurs in some forms (typically in dry, well-drained habitats). Plants are typically short and shrubby but may grow to several meters in the absence of disturbance _____ var. **obovalis**

Petals (7.6–)8.8(–11) mm long and (3.1–)3.7(–4.3) mm wide, inflorescences at peak flower (43.9–)47.8(–51.7) mm, elongating in fruit to (43.2–)48.2 (–53.2) mm, lowest pedicels (flowering) 15.8(14.1)–(17.5) mm, elongating in fruit to (15.1–)17.5 (–19.9) mm. Inflorescences using widely spreading, the lowest pedicel averaging 36% of the total inflorescence length at flowering, and 38% in fruit. Leaves on older branches chiefly broadly elliptical or occasionally oblong, the widest point at 49–55% of the total leaf length. Sepals usually spreading to reflexed in flower and in fruit. Ovary summit glabrous. Plants are typically multi-stemmed with tall slender branches _____ var. **canadensis**

ACKNOWLEDGMENTS

I am grateful to Art Tucker, director, Robert Naczi, curator, and Keith Clancy, collections manager, of the Claude E. Phillips Herbarium (DOV), Delaware State Univ., Dover, DE for managing loans of herbarium material and providing access to a beautiful facility. During the term of this research I have borrowed material from a number of institutions and I would like to thank the curators and staff at: CM, FLAS, GA, MARY, NA, NCU, PH, US, USCH, VPI, and WVA, who so efficiently handled the distribution of material to Dover. I would like to offer special thanks to Alain Changy (P) and Mark Spencer (LINN) who provided images of type specimens held in Paris and London, respectively. Gwen Brewer, Wesley Knapp and William McAvoy provided helpful comments on early drafts of the manuscript. Jason Harrison and Wesley Knapp assisted with fieldwork. Dan Siehl, with an artists care, mounted and processed hundreds of *Amelanchier* vouchers at the Tawes Herbarium, Maryland Department of Natural Resources, Annapolis, MD. The Maryland Department of Natural Resources, Natural Heritage Program, the Claude E. Phillips Herbarium, Delaware State University and the Norton-Brown Herbarium, University of Maryland, College Park supported this research. Christopher Campbell, University of Maine, and an anonymous reviewer provided critical comments that greatly improved this manuscript.

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